Pedobiologia **26**, 309—330 (1984)

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# Population dynamics and production studies of species of Euglyphidae (Testacea, Rhizopoda, Protozoa) in an aspen woodland soil

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With 6 figures

(Accepted: 83-06-10)

## 1. Introduction

The importance of soil Testacea has been the object of considerable speculation but little intensive study in the past. For example, poorly known aspects of testacean ecology are annual population dynamics, secondary production, biomass turnover and impact on the organic cycle. Species of the family Euglyphidae have received some detailed study on taxonomy (DECLOITRE 1962, 1976, 1979, 1981, 1982; COÛTEAUX 1979; OGDEN 1981), geographical distribution (WAILES & PENARD 1911; DE GRAAF 1956; BONNET & THOMAS 1960; DECLOITRE 1962, 1976, 1979, 1981, 1982; LOUSIER 1976), basic biology (CARTER 1865; PENARD 1890; WAILES 1915; HALL & LOEFER 1930; HEDLEY & OGDEN 1973, 1974a, b; HEDLEY *et al.* 1974), and test structure and reproduction (NETZEL 1972, 1977a, b), but limited study with regard to population ecology. SMITH (1973) provided monthly estimates of the density of *Corythion dubium* TARANEK in an Antarctic peat site. Biweekly density estimates for 11 species of Euglyphidae were obtained by SCHÖNBORN (1975) for a coniferous and a deciduous forest soil. Other studies have attempted to estimate densities, biomass, secondary production, biomass turnover and generation times for other Testacea as well as the Euglyphidae (LOUSIER 1974 a, b; SCHÖNBORN 1975, 1977, 1978, 1982/3; COÛTEAUX 1976, 1978; LAMINGER *et al.* 1980; FOISSNER & ADAM 1981). However, there has been no reporting of an intensive population study of the Euglyphidae which details (1) the annual variation in total density, biomass, production and turnover in each of the soil and litter layers, (2) the relationship of the Euglyphidae to the total testacean community, and (3) the relative importance of the Euglyphidae in the soil and litter. It is the intention of this paper to report the results of such a study which was carried out in a cool temperate deciduous woodland and lasted for 57 weeks.

## 2. Site and methods

### 2.1. Site location and description

The general study area comprised about 21 km² at the northern end of the Kananaskis Valley in the Fisher Range of the Rocky Mountains of Alberta, Canada. LOUSIER (1974a, 1975) and LOUSIER & PARKINSON (1976, 1978, 1979) have provided detailed descriptions of the site, including additional information on the soil, vegetation, meteorology, litter input, litter decomposition and litter and soil chemistry.

To briefly summarize then, the study site was an aspen woodland located at 1,400 m ASL on a well-drained, south-facing slope. The climate is essentially continental, characterized by short, dry summers and relatively long, cold winters with intermittent, warm, chinook winds. The soil has been classified in the orthic gray luvisol subgroup, with a surface organic horizon (mor) easily separated into L (whole litter), F (fragmented litter), H (humus) and Ah (black mineral) layers (LOUSIER 1974a). The canopy was dominated by trembling aspen (*Populus tremuloides* MICHX.) with balsam poplar (*P. balsamifera* L.) being less frequent in occurrence. Various grasses, herbs and wild rose shrubs were the main components of the understory.

Table 1. Occurrence, distribution, biomass (mg $10^{-6}$ cells) and constancy of species of Euglyphidae in the organic layers of the aspen woodland soil

| Species observed | Biomass | No. of cells measured | Distribution | | | | Constancy (%)[c] | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | L | F | H | Ah | L | F | H | Ah |
| *Euglypha laevis* (Ehrenberg) Perty | 3.8 ± 0.3[a] | 100 | [b] +/+ | +/+ | +/+ | +/+ | 100 | 100 | 100 | 32 |
| *E. rotunda* Wailes et Penard | 3.5 ± 0.3 | 100 | +/+ | +/+ | +/+ | +/+ | 100 | 100 | 100 | 30 |
| *E. scutigera* Penard | 7.6 ± 0.5 | 100 | +/+ | +/+ | +/+ | +/+ | 100 | 100 | 100 | 100 |
| *E. cuspidata* Bonnet | 1.5 ± 0.1 | 100 | +/+ | +/+ | +/+ | —/+ | 100 | 100 | 100 | 0 |
| *E. compressa* Carter | 24.1 ± 1.0 | 30 | +/+ | +/+ | —/+ | —/— | 22 | 10 | 0 | 0 |
| *E. compressa f. glabra* Wailes | 24.1 ± 1.1 | 30 | +/+ | +/+ | —/+ | —/— | 22 | 22 | 0 | 0 |
| *E. polylepis* (Bonnet) Decloitre | 8.8 ± 0.6 | 10 | —/— | —/+ | +/+ | —/+ | 0 | 0 | 16 | 0 |
| *Trinema lineare* Penard | 2.0 ± 0.2 | 100 | +/+ | +/+ | +/+ | +/+ | 100 | 100 | 100 | 100 |
| *T. enchelys* (Ehrenberg) Leidy | 9.8 ± 0.6 | 100 | +/+ | +/+ | +/+ | +/+ | 100 | 100 | 100 | 96 |

[a] Standard Error

[b] Observed as living/observed as empty tests

[c] Constancy: Species observed in > 50 % of samples — constant in frequency; Species observed in 25—50 % of samples — incidental in frequency; Species observed in < 25 % of samples — accidental in frequency (Coûteaux 1976).

### 2.2. Sampling and analysis

The arrangement of the study plots in the aspen woodland site has been illustrated in LOUSIER & PARKINSON (1979); the sample preparation techniques and sample examination procedures were outlined in LOUSIER & PARKINSON (1981a); and the sampling program and population analysis equations have been detailed in LOUSIER (1984).

## 3. Results

### 3.0. General

Nine species of Euglyphidae were observed as live cells or empty tests throughout the study period in the aspen woodland soil (Table 1). Only 6 of these species could be considered constant in frequency (*sensu* COÛTEAUX 1976); three others were either incidental or accidental (Table 1). Only the six constant species were subjected to the detailed population analysis. Table 1 also presents the biomass (wet mass $10^{-6}$ cells) measured for each species of Euglyphidae recorded in the study period. Estimates of the live mass of an individual cell were made by calculating the volume of the cell and assuming a specific gravity of about 1.0 (HEAL 1970). The estimates were made primarily on live individuals isolated from field samples with some augmenting measurements from the COÛTEAUX slides. There was no observed seasonal or spatial variation in cell size or biomass. The estimates given in Table 1 compare favourably with those for the Euglyphidae from moder humus examined by SCHÖNBORN (1975, 1977, 1978) but are substantially less than the estimates given in SCHÖNBORN (1982) for mull humus.

Only *E. laevis*, *E. rotunda*, *E. scutigera*, *T. lineare*, and *T. enchelys* were found living in all 4 soil layers. *E. cuspidata* was not observed as living in the Ah layer and, in fact, decreased in abundance from the L to the H layer (Fig. 4). This species was one of the two initial colonizing species on aspen and balsam poplar litter (LOUSIER 1982) and appeared to favour the litter environment. *E. compressa* and *E. compressa f. glabra*, found only in the L and F layers, were also early colonizers and decreased in abundance with the age of the litter (LOUSIER 1982). *E. polylepis* was sparse in number, a late colonizer and also increased in number with litter age. This may help explain the presence of live *E. polylepis* in only the H layer.

### *3.1. Euglypha laevis*

The weekly fluctuations in abundance of active, encysted and empty tests are illustrated in Fig. 1 and the population data are summarized in Table 2. The fluctuations of living *E. laevis* throughout the year were similar in pattern in the F, H and Ah layers; there were no evident or statistical relationships between the fluctuations in abundance and soil moisture variation. Active and encysted L-layer *E. laevis* fluctuated quite differently from the numbers in the other layers during the study period. The May—June drop and subsequent increase in the abundance of active forms in the L layer occurred simultaneously with an identical pattern in L-layer moisture fluctuations. The response of the active population to the increasing moisture content produced the highest reproductive rate and one of the highest biomass turnover rates recorded for the year. There was, however, no strong statistical relationship at this time between population fluctuations and litter moisture changes.

Rate of natural increase (r), biomass production ($P_B$) and biomass turnover ($P_B/B$) were highest in spring in the L and Ah layers and showed no seasonal trends in the H layer. No seasonal trends were the rule in the F layer except that biomass turnover had peaks in spring, summer and fall only. The fastest generation times recorded were: L — 2.0 days (mid-June), F — 1.0 day (mid-July), H — 1.1 days (late February), and Ah — 2.0 days (mid-June). *E. laevis* appeared to favour the litter environment in that the species had higher relative density and biomass in the L and F layers and was ranked low relative to all the species in terms of production statistics in the Ah layer. However, it has its highest $P_N$, $P_B$ and T in the H layer (Table 2) and was ranked second highest of all species in r and $P_B/B$ for the H layer. *E. laevis* accounted for about 5% of the annual Euglyphidae $P_B$ and 3% of the total annual $P_B$ in the aspen woodland soil.

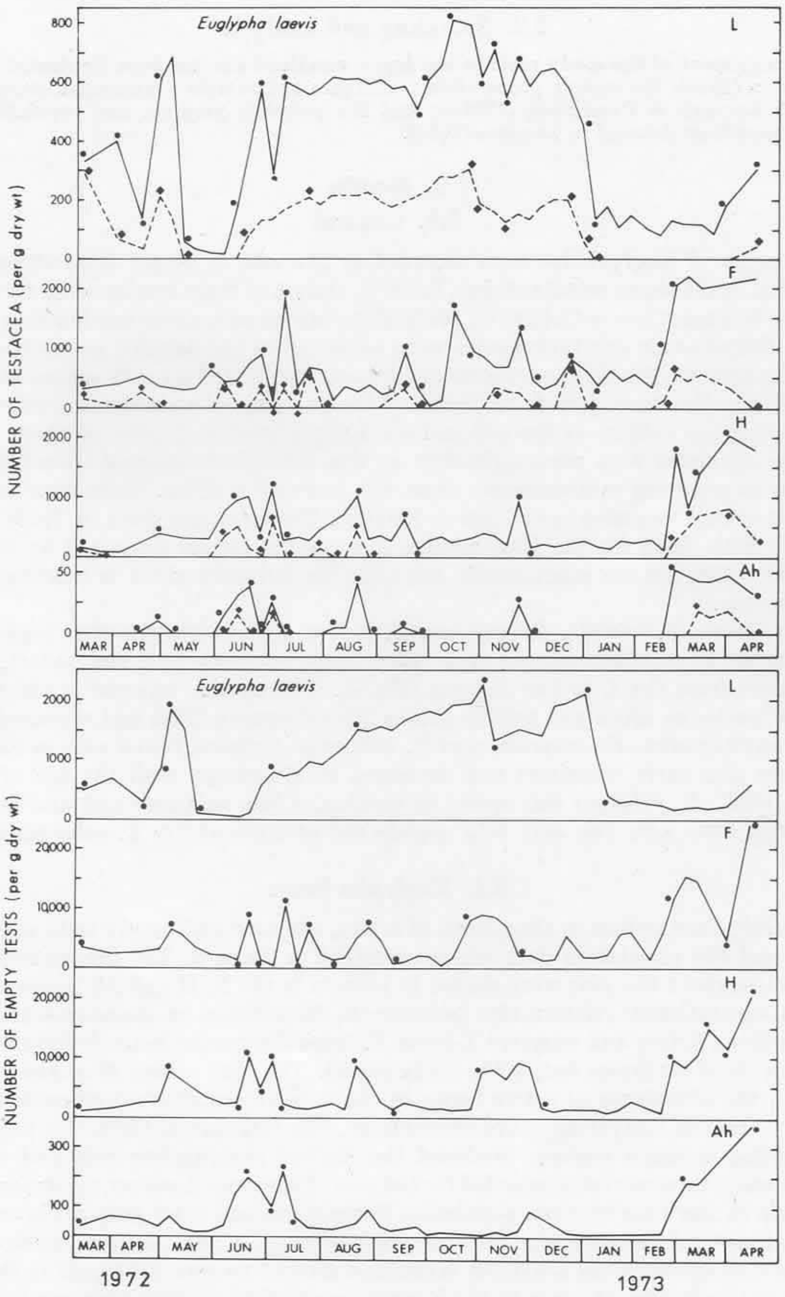


Fig. 1. The annual fluctuations of numbers of active, encysted and empty tests of *Euglypha laevis* (---- encysted tests; ● indicates significant difference from previous ● for active or empty tests; ◆ indicates significant difference from previous ◆ for encysted tests).

Table 2. Summary of the population parameters calculated for *Euglypha laevis*

| | L | F | H | Ah |
|---|---|---|---|---|
| Annual mean density (D) ($\times 10^6$ m$^{-2}$) | 0.47 ± 0.04*) | 1.66 ± 0.19 | 2.22 ± 0.27 | 0.04 ± 0.01 |
| Annual mean relative density (RD) (%) | 2.77 ± 0.19 | 2.91 ± 0.25 | 1.96 ± 0.24 | 0.67 ± 0.05 |
| Annual mean biomass (B) (mg m$^{-2}$) | 1.78 ± 0.16 | 6.80 ± 0.85 | 8.15 ± 0.99 | 1.35 ± 0.10 |
| Annual mean relative biomass (RB) (%) | 4.29 ± 0.46 | 3.28 ± 0.32 | 2.40 ± 0.22 | 1.11 ± 0.05 |
| Production numbers ($P_N$) ($\times 10^6$ m$^{-2}$ y$^{-1}$) | 56.89 | 562.01 | 951.63 | 37.68 |
| Annual mean r (day$^{-1}$) | 0.015 ± 0.08 | 0.249 ± 0.021 | 0.276 ± 0.016 | 0.200 ± 0.013 |
| Annual mean generation time (T) (days) | 9.6 ± 1.5 | 5.5 ± 0.9 | 3.1 ± 0.3 | 15.9 ± 4.7 |
| Number of generations (G) (y$^{-1}$) | 56.8 | 118.4 | 130.5 | 26.6 |
| Annual mean mortality (M) (% day$^{-1}$) | 9.0 ± 0.3 | 11.0 ± 0.3 | 11.9 ± 0.2 | 12.9 ± 0.3 |
| Production biomass ($P_B$) (mg m$^{-2}$ y$^{-1}$) | 216.2 | 2,135.6 | 3,616.2 | 143.2 |
| Annual mean $P_B/B$ (week$^{-1}$) | 2.5 ± 0.3 | 12.6 ± 4.7 | 11.8 ± 2.0 | 6.1 ± 0.5 |

*) Standard error.

Table 3. Summary of the population parameters calculated for *Euglypha rotunda*

| | L | F | H | Ah |
|---|---|---|---|---|
| Annual mean density (D) ($\times 10^6$ m$^{-2}$) | 0.20 ± 0.02*) | 2.45 ± 0.38 | 2.74 ± 0.44 | 0.08 ± 0.02 |
| Annual mean relative density (RD) (%) | 1.16 ± 0.11 | 3.59 ± 0.36 | 1.90 ± 0.24 | 1.12 ± 0.10 |
| Annual mean biomass (B) (mg m$^{-2}$) | 0.70 ± 0.06 | 9.09 ± 1.51 | 8.68 ± 1.34 | 0.71 ± 0.21 |
| Annual mean relative biomass (RB) (%) | 1.73 ± 0.20 | 3.56 ± 0.42 | 2.32 ± 0.27 | 1.68 ± 0.11 |
| Production numbers ($P_N$) ($\times 10^6$ m$^{-2}$ y$^{-1}$) | 18.94 | 922.54 | 1,053.63 | 69.80 |
| Annual mean r (day$^{-1}$) | 0.092 ± 0.008 | 0.287 ± 0.028 | 0.248 ± 0.021 | 0.182 ± 0.014 |
| Annual mean generation time (T) (days) | 11.4 ± 1.5 | 4.9 ± 0.7 | 6.7 ± 1.6 | 6.1 ± 1.3 |
| Number of generations (G) (y$^{-1}$) | 48.6 | 143.1 | 131.4 | 34.1 |
| Annual mean mortality rate (M) (% day$^{-1}$) | 8.2 ± 0.19 | 11.3 ± 0.27 | 10.8 ± 0.29 | 13.1 ± 0.24 |
| Production biomass ($P_B$) (mg m$^{-2}$ y$^{-1}$) | 66.3 | 3,228.9 | 3,687.7 | 244.3 |
| Annual mean $P_B/B$ (week$^{-1}$) | 2.3 ± 0.35 | 22.1 ± 8.0 | 8.1 ± 1.14 | 4.3 ± 0.99 |

*) standard error

### 3.2. *Euglypha rotunda*

*E. rotunda* is structurally very similar to *E. laevis* and had a biomass almost identical to that for *E. laevis* (Table 1). *E. rotunda* was less abundant than *E. laevis* in the L layer but slightly more abundant in the F, H and Ah layers (Fig. 2). The patterns of fluctuations in

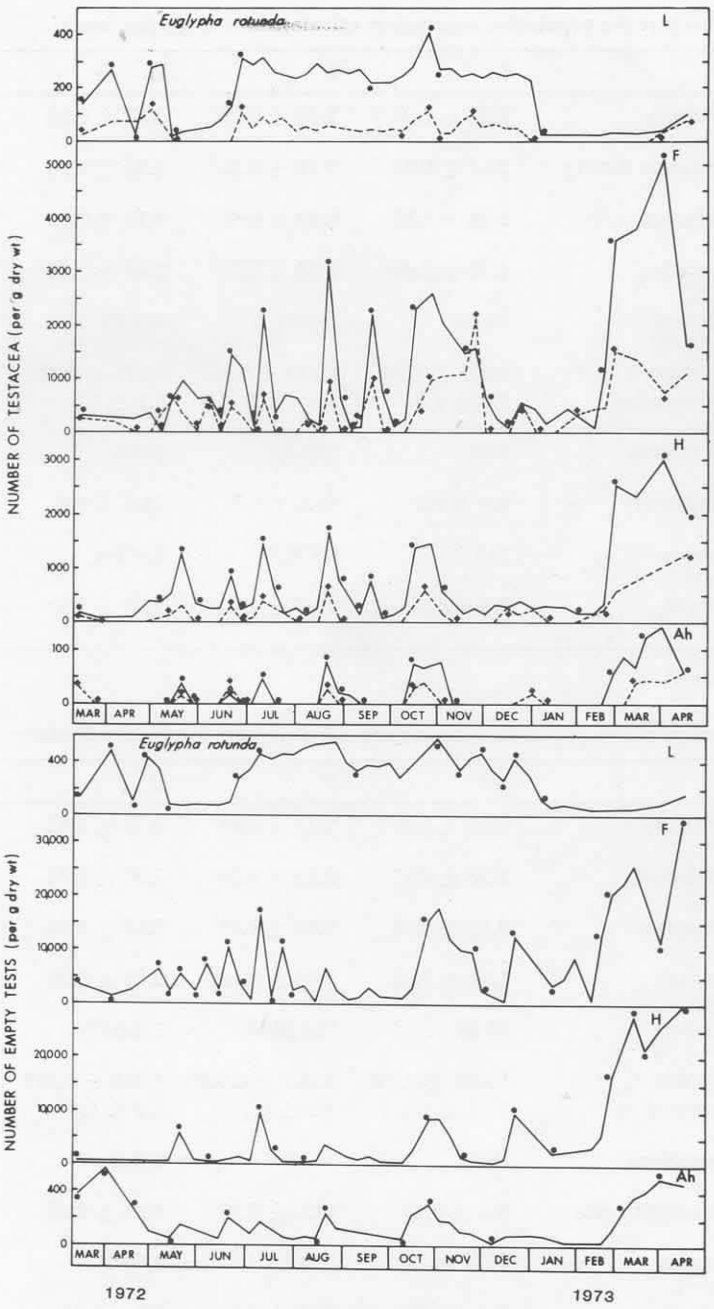


Fig. 2. The annual fluctuations of numbers of active, encysted and empty tests of *Euglypha rotunda* (----- encysted tests; ● indicates significant difference from previous ● for active or empty tests; ◆ indicates significant difference from previous ◆ for encysted tests).

numbers were very similar but the magnitude of the fluctuations for active *E. rotunda* was slightly greater. Active *E. rotunda* in the L layer responded to the May—June moisture dip in a pattern similar to that of *E. laevis* but the recovery response in *E. rotunda* was slower.

The summary of the population data in Table 3 indicates that in the L and Ah layers, r, $P_B$ and $P_B/B$ were highest in early spring and fall; in the F and H layers, r and $P_B$ showed no seasonal trends but $P_B/B$ was highest at various times throughout the summer and late autumn. The most rapid generation times were: L — 2.4 days (early May), F — 0.9 day (mid-July), H — 1.2 days (late February), and Ah — 1.7 days (early April). Based on the data in Table 3 and the rankings of all the species, *E. rotunda* appeared to be more successful in terms of production and turnover in the F and H layers. For example, the $P_B/B$ recorded for the F-layer population was the highest recorded in the study. About 6% of the annual euglyphid $P_B$ and 3.5% of the total annual testacean $P_B$ was attributable to *E. rotunda*.

### 3.3. *Euglypha scutigera*

The population level of active *E. scutigera* in the L layer was fairly even throughout the year except for an extended peak after leaf fall (Fig. 3). The number of active forms more than quadrupled but then returned to the prefall level in late November. The population levels in the other layers also peaked after leaf fall but the elevated levels were not maintained as long and this peak was only one of a series of peaks during the study period. This species had a greater relative proportion of cysts than did the other *Euglypha* spp. and there was some indication of an inverse relationship between numbers of active forms and numbers of encysted forms. The prominent peaks in cyst abundance in April 1972 in the F, H and Ah layers coincided with peaks in r, $P_B$ and $P_B/B$. It was possible that the complete or near complete encystation of a population during a period of high production and turnover was caused by increased levels of free soil water due to the advanced stages of snow-melt and increasing soil and litter temperatures (LOUSIER 1984) inhibiting cellular activity.

L- and Ah-layer levels of r, $P_B$ and $P_B/B$ were maximum in the spring and fall while F-layer levels showed no seasonal trends. The reproductive rate showed no seasonal trends in the H layer, but $P_B$ and $P_B/B$ peaked only in spring, summer and fall. The fastest generation

Table 4. Summary of the population parameters calculated for *Euglypha scutigera*

| | L | F | H | Ah |
|---|---|---|---|---|
| Annual mean density (D) ($\times 10^6$ m$^{-2}$) | 0.18 ± 0.03*) | 0.29 ± 0.05 | 1.5 ± 0.27 | 0.42 ± 0.06 |
| Annual mean relative density (RD) (%) | 1.27 ± 0.13 | 0.65 ± 0.12 | 1.14 ± 0.17 | 3.43 ± 0.46 |
| Annual mean biomass (B) (mg m$^{-2}$) | 1.39 ± 0.23 | 2.18 ± 0.35 | 10.33 ± 1.75 | 10.64 ± 1.56 |
| Annual mean relative biomass (RB) (%) | 2.95 ± 0.29 | 1.15 ± 0.16 | 2.88 ± 0.37 | 8.92 ± 0.92 |
| Production numbers ($P_N$) $\times 10^6$ m$^{-2}$ y$^{-1}$) | 20.16 | 121.16 | 284.32 | 326.04 |
| Annual mean r (day$^{-1}$) | 0.108 ± 0.010 | 0.308 ± 0.027 | 0.182 ± 0.014 | 0.151 ± 0.011 |
| Annual mean generation time (T) (days) | 9.7 ± 1.0 | 4.7 ± 0.8 | 6.6 ± 1.1 | 7.5 ± 1.2 |
| Number of generations (G) (y$^{-1}$) | 53.1 | 145.7 | 87.1 | 71.8 |
| Annual mean mortality rate (M) (% day$^{-1}$) | 9.2 ± 0.1 | 12.2 ± 0.2 | 10.2 ± 0.3 | 9.4 ± 0.3 |
| Production biomass ($P_B$) (mg m$^{-2}$ y$^{-1}$) | 153.2 | 920.8 | 2,160.8 | 2,477.9 |
| Annual mean $P_B/B$ (week$^{-1}$) | 2.8 ± 0.4 | 20.4 ± 4.4 | 4.3 ± 0.5 | 3.6 ± 0.5 |

*) standard error

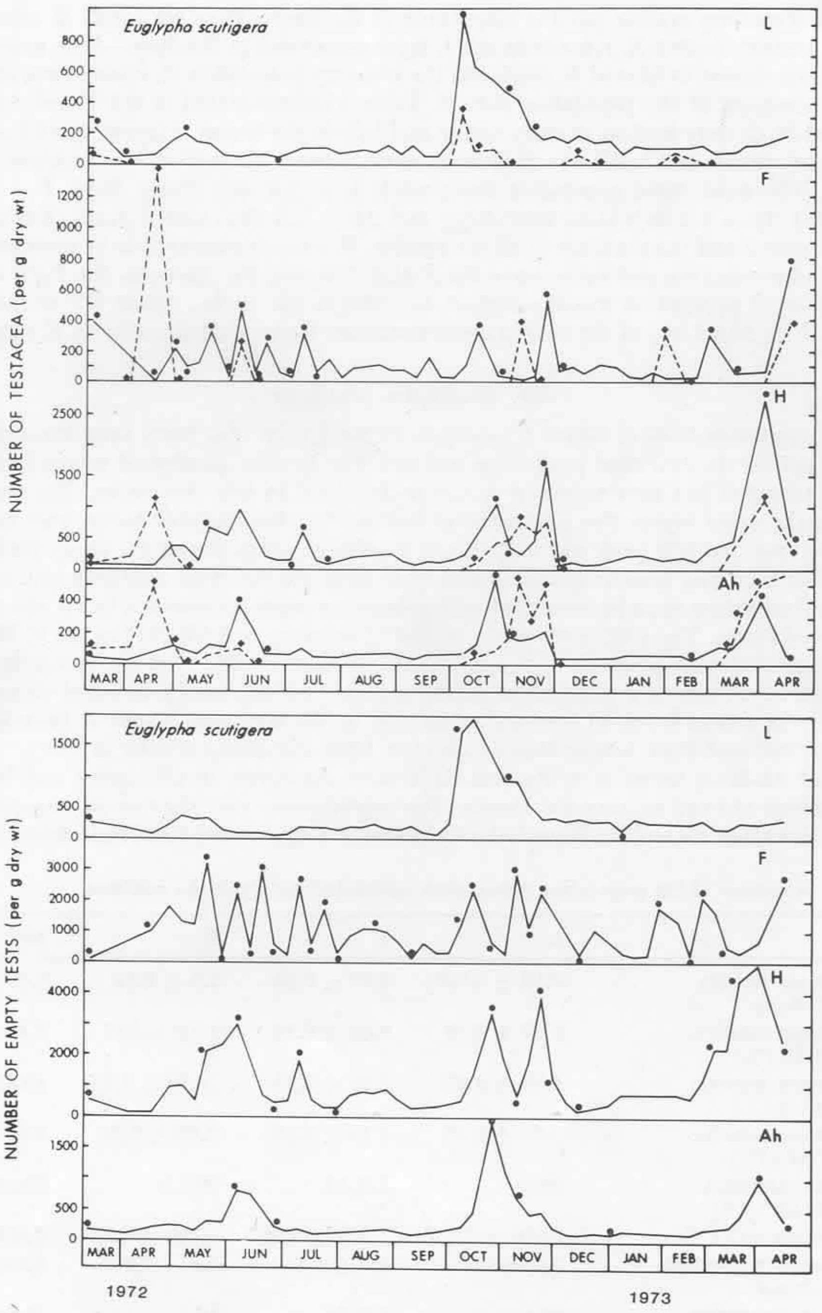


Fig. 3. The annual fluctuations of numbers of active, encysted and empty tests of *Euglypha scutigera* (----- encysted tests; ● indicates significant difference from previous ● for active or empty tests; ◆ indicates significant difference from previous ◆ for encysted tests).

times recorded were: L — 1.6 days (mid-October), F — 1.0 day (mid-July), H — 1.8 days (late May, mid-July) and Ah — 2.1 days (early June, late October). $P_B$ increased with depth to the Ah layer — *E. scutigera* was the only species to do so (Table 4). Compared to the other 13 constant species in the testacean community, *E. scutigera* had the highest r and G, lowest D and RD, and the second highest $P_B/B$ for the F layer. *E. scutigera* was near the lower end of the range for biomass turnover in the L, H and Ah layers, and represented about 3% of the total annual testacean production biomass and 4.5% of the euglyphid $P_B$ (Table 4).

### 3.4. Euglypha cuspidata

The graphs of active *E. cuspidata* in each layer had two similarities: a post-leaf fall peak and an early spring 1973 peak (Fig. 4). An interesting aspect of the post-leaf fall peaks was that they were not coincident, i.e., the F-layer peak occurred three weeks after the L peak and the H peak occurred two weeks later than the F-layer peak. The early spring 1973 peaks and the post-leaf fall peaks occurred when soil temperatures were similar, i.e., just above the freezing mark. The mid-spring 1972 peak in the L layer occurred during the major May—June litter moisture content drop. The population of active *E. cuspidata* grew until litter moisture levels dropped to about 55%; as the moisture level continued to drop, the population also fell substantially.

*E. cuspidata* was the only species in which the annual mean population density and biomass decreased with depth (Table 5). D, B and $P_N$ in the L layer were the highest for any of the *Euglypha* spp. and in the top third in comparison with the 13 other constant species. Despite this obvious abundance in the L layer, this species was only third overall in production in the L layer. *E. cuspidata* production in the F and H layers was second from the lowest ranking for all the species. Generation times decreased with depth and r, G and $P_B/B$ were highest in the F layer. Compared to the other constant species, *E. cuspidata* was in the top third in terms of r, G and $P_B/B$ in the F and H layers.

The rate of increase was highest in summer in the L layer and had no seasonal trends in the F and H layers. $P_B$ peaked in the spring and fall in the L and F layers, and spring, summer and fall in the H layer. $P_B/B$ was highest during late spring and summer in all the layers.

Table 5. Summary of the population parameters calculated for *Euglypha cuspidata*

| | L | F | H | Ah |
|---|---|---|---|---|
| Annual mean density (D) ($\times 10^6$ m$^{-2}$) | 1.25 ± 0.13*) | 0.72 ± 0.11 | 0.71 ± 0.07 | — |
| Annual mean relative density (RD) (%) | 7.41 ± 0.58 | 1.33 ± 0.23 | 0.74 ± 0.16 | — |
| Annual mean biomass (B) (mg m$^{-2}$) | 1.87 ± 0.21 | 1.13 ± 0.20 | 0.98 ± 0.10 | — |
| Annual mean relative biomass (RB) (%) | 3.88 ± 0.36 | 0.50 ± 0.06 | 0.31 ± 0.03 | — |
| Production numbers ($P_N$) ($\times 10^6$ m$^{-2}$ y$^{-1}$) | 193.6 | 258.1 | 314.1 | — |
| Annual mean r (day$^{-1}$) | 0.135 ± 0.012 | 0.284 ± 0.023 | 0.263 ± 0.015 | — |
| Annual mean generation time (T) (days) | 11.4 ± 3.0 | 5.7 ± 1.5 | 3.6 ± 0.4 | — |
| Number of generations (G) (y$^{-1}$) | 66.0 | 136.6 | 126.0 | — |
| Annual mean mortality rate (M) (% day$^{-1}$) | 9.9 ± 0.18 | 12.1 ± 0.20 | 11.9 ± 0.19 | — |
| Production biomass ($P_B$) (mg m$^{-2}$ y$^{-1}$) | 290.4 | 387.1 | 471.1 | — |
| Annual mean $P_B/B$ (week$^{-1}$) | 3.9 ± 0.7 | 16.9 ± 4.2 | 9.1 ± 1.1 | — |

*) standard error

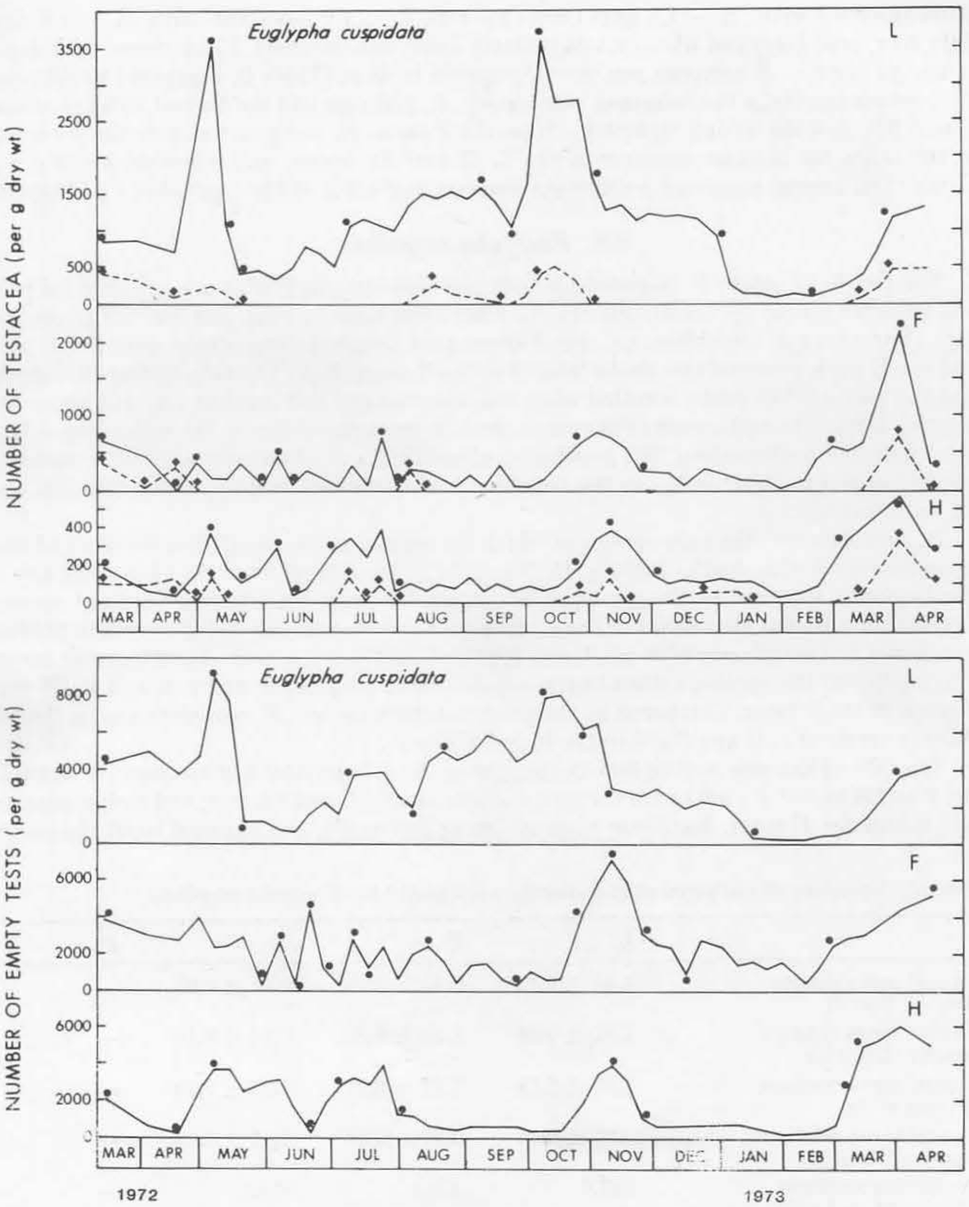


Fig. 4. The annual fluctuations of numbers of active, encysted and empty tests of *Euglypha cuspidata* (----- encysted tests; ● indicates significant difference from previous ● for active or empty tests; ◆ indicates significant difference from previous ◆ for encysted tests).

The fastest generation times observed were: L — 1.4 days (mid-August), F — 1.0 day (mid-July), and H — 1.5 days (mid- and late May, late June). *E. cuspidata* accounted for about 0.6% of the total annual secondary production and about 1% of the Euglyphidae $P_B$.

### 3.5. *Trinemia lineare*

The weekly fluctuations in numbers of active, encysted and empty tests are shown in Fig. 5 and the population parameters are summarized in Table 6. *T. lineare* can be described

Table 6. Summary of the population parameters calculated for *Trinema lineare*

| | L | F | H | Ah |
|---|---|---|---|---|
| Annual mean density (D) ($\times 10^6$ m$^{-2}$) | 1.84 ± 0.33*) | 14.23 ± 3.78 | 35.63 ± 8.80 | 2.51 ± 0.43 |
| Annual mean relative density (RD) (%) | 11.24 ± 1.46 | 16.62 ± 1.66 | 17.50 ± 1.68 | 14.51 ± 1.16 |
| Annual mean biomass (B) (mg m$^{-2}$) | 3.80 ± 0.76 | 30.16 ± 8.96 | 60.53 ± 14.20 | 16.18 ± 2.84 |
| Annual mean relative biomass (RB) (%) | 5.79 ± 0.68 | 11.09 ± 1.67 | 13.74 ± 1.78 | 12.25 ± 1.30 |
| Production numbers ($P_B$) ($\times 10^6$ m$^{-2}$ y$^{-1}$) | 728.8 | 3,464.3 | 6,260.2 | 3,368.8 |
| Annual mean r (day$^{-1}$) | 0.214 ± 0.018 | 0.237 ± 0.023 | 0.224 ± 0.014 | 0.230 ± 0.011 |
| Annual mean generation time (T) (days) | 4.8 ± 0.63 | 4.8 ± 0.61 | 4.3 ± 0.47 | 3.8 ± 0.57 |
| Number of generations (G) (y$^{-1}$) | 104.7 | 119.9 | 107.3 | 110.6 |
| Annual mean mortality rate (M) (% day$^{-1}$) | 11.5 ± 0.16 | 11.4 ± 0.24 | 11.4 ± 0.22 | 11.9 ± 0.08 |
| Production biomass ($P_B$) (mg m$^{-2}$ y$^{-1}$) | 1,457.6 | 6,928.6 | 1,5220.3 | 6,737.5 |
| Annual mean ($P_B/B$) (week$^{-1}$) | 7.4 ± 1.7 | 8.8 ± 1.6 | 5.2 ± 0.6 | 6.4± 1.7 |

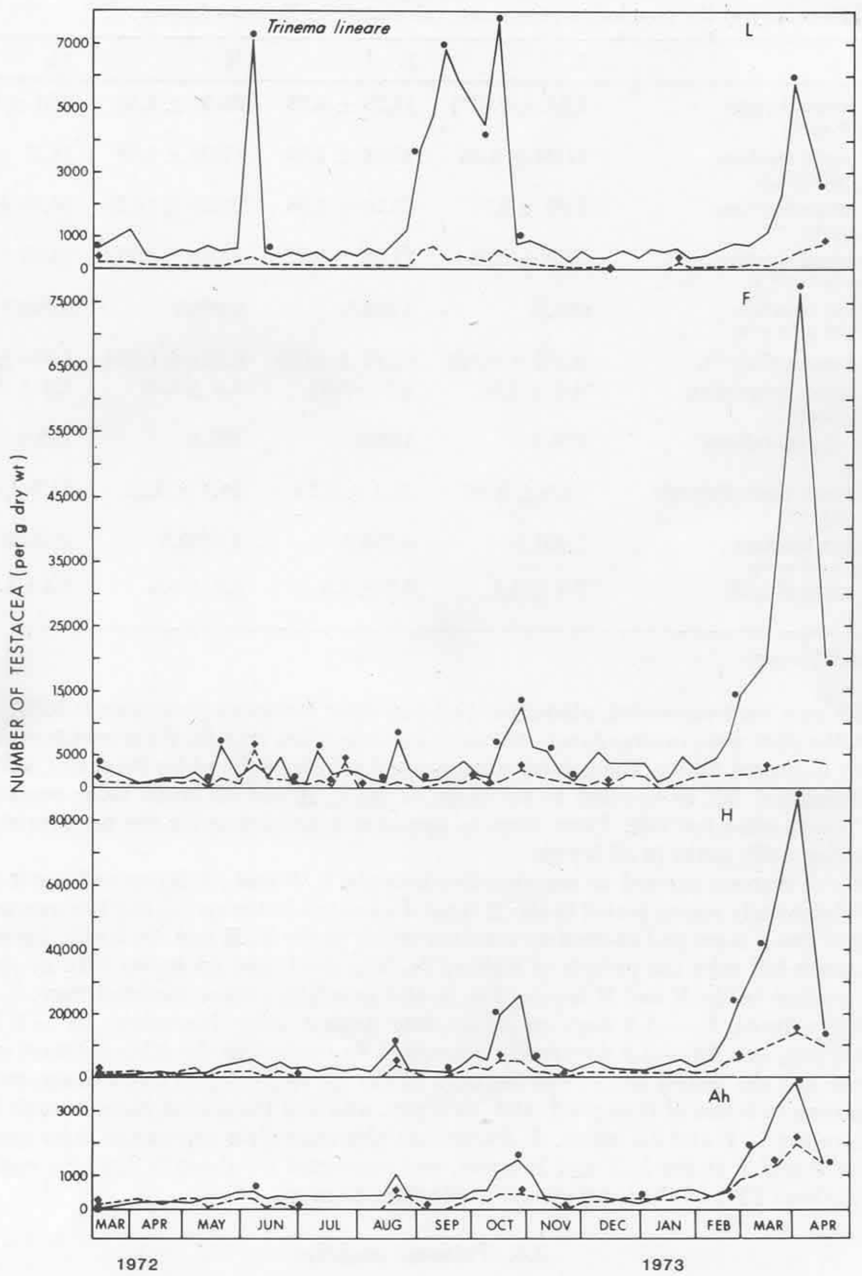
*) standard error

generally as a very successful, ubiquitous soil and litter testacean (SCHÖNBORN 1983). In the L layer, the June peak in abundance of active forms coincided with the litter moisture content recovery discussed above. The L layer population was distinguished by its major, sustained peak **during** leaf fall as opposed to the peaks in the F, H and Ah layers being recorded up to one month after leaf fall. There were no apparent explanations for the magnitude of the early spring 1973 peaks in all layers.

Rates of increase showed no seasonal trends in the L, F and Ah layers and lower values in the winter-early spring period in the H layer. $P_B$ peaked in the spring and late summer-fall periods in the L layer and showed no seasonal trends in the F, H and Ah layers. Spring and late summer-fall were the periods of highest $P_B/B$ in the L and Ah layers with no seasonal trends evident in the F and H layers. The fastest generation times recorded were: L — 1.2 days (early June), F — 1.3 days (mid-July, late August, early December), H — 1.7 days (mid-August), and Ah — 1.9 days (early February). In relation to the other constant species, *T. lineare* had the fastest and second fastest T in the Ah and L layers respectively, was near the top rank in terms of G in the L and Ah layers, and had the second highest totals for $P_N$ and $P_B$ in the L, F and Ah layers. *T. lineare* was also among the top two or three species in terms of D and B in the L, F and H layers, and accounted for about 21% of the euglyphid $P_B$ and about 13% of the total annual production biomass.

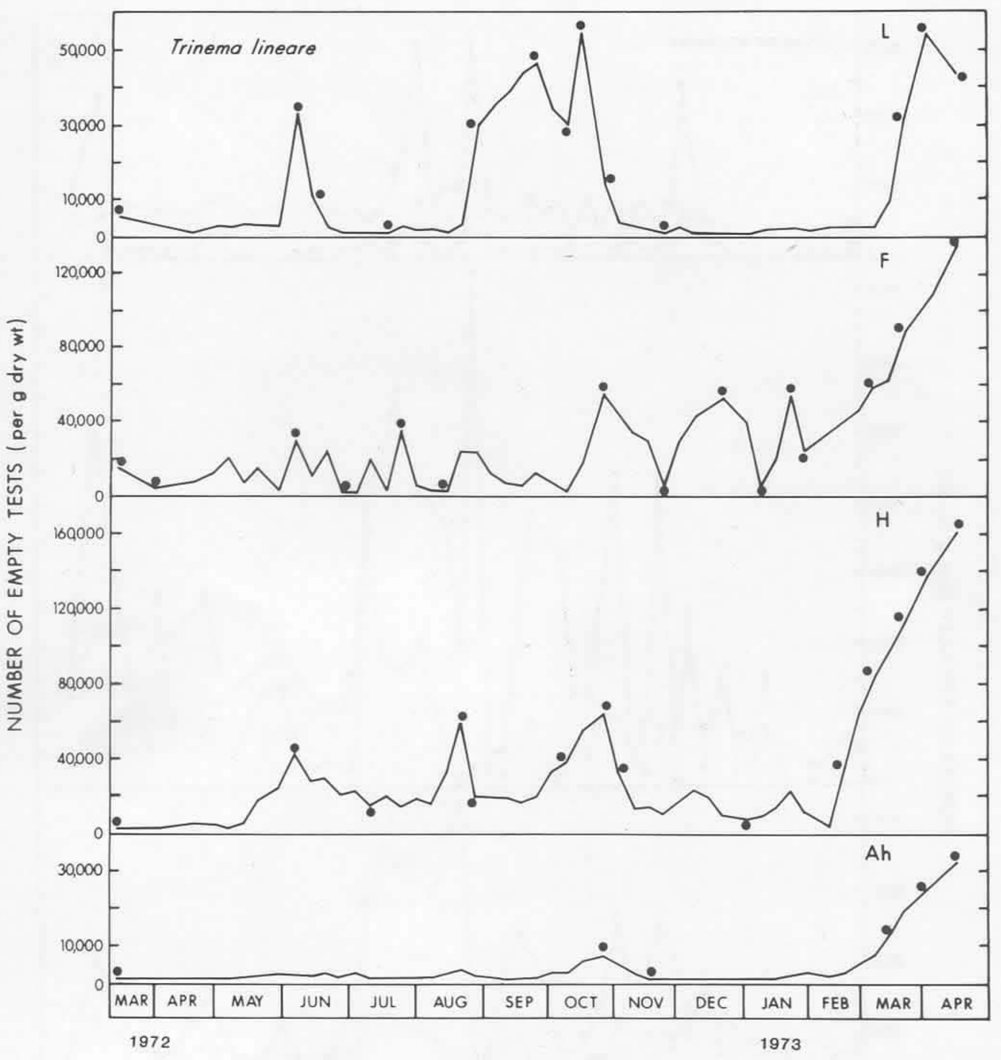
### 3.6. *Trinema enchelys*

This is another very successful, ubiquitous species (SCHÖNBORN 1983), that was less abundant than *T. lineare* but had a cellular biomass five times greater (Table 1) and an annual mean biomass about 60% higher (Table 7). The population fluctuations in the L layer illustrated in Fig. 6 were very similar in pattern to those for *T. lineare* (Fig. 5) and peaked essentially at the same time. The major exception was the behavior of the *T. lineare* population during leaf fall — the population peaked at the initiation of leaf fall and then abruptly fell an equivalent amount. The population then peaked again at the end of leaf fall. The F, H and Ah layer population graphs are dominated by major sustained peaks throughout leaf fall and into mid-fall. The F-layer population was subject to frequent, large fluctuations throughout the



5 A

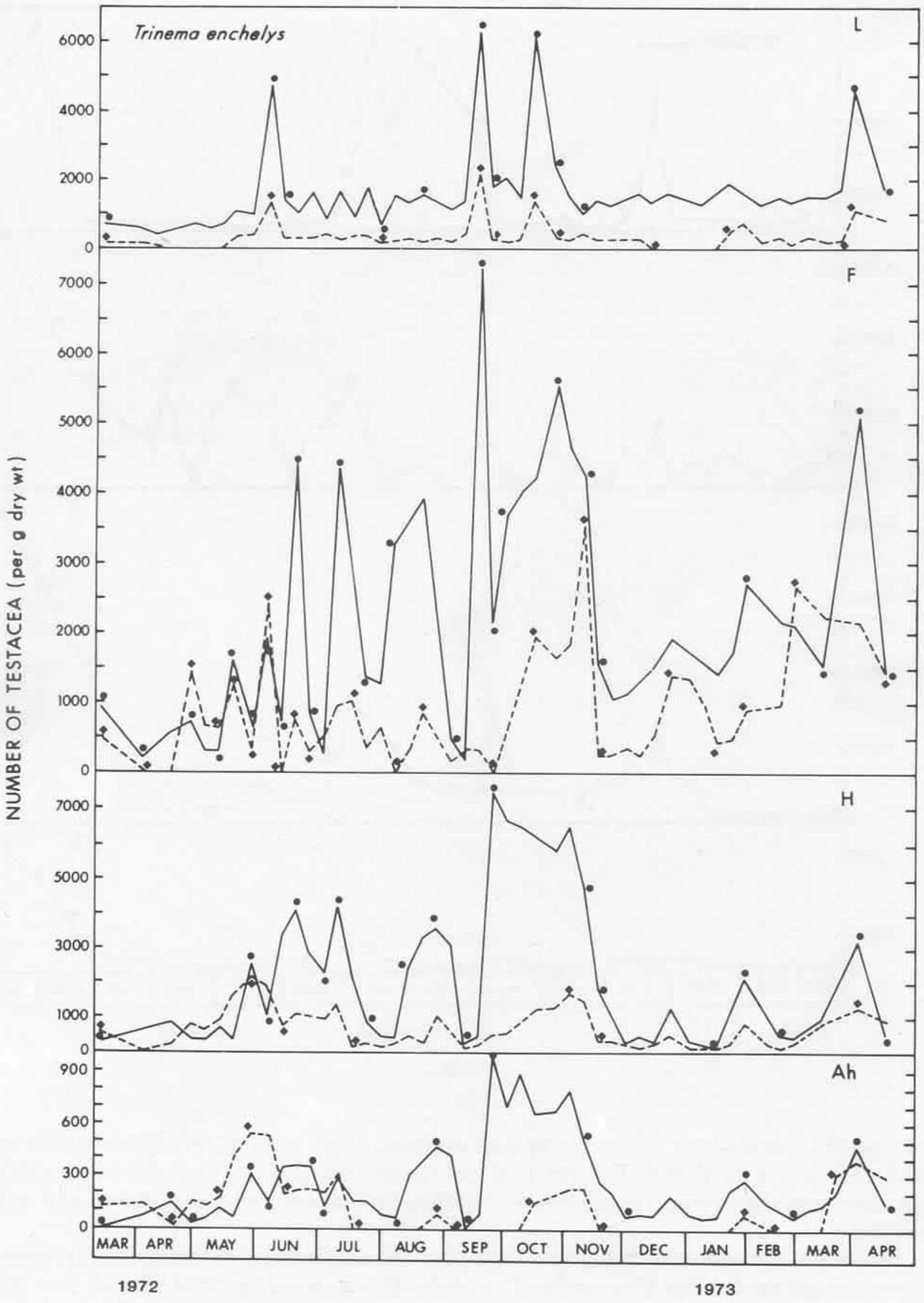
Fig. 5. The annual fluctuations of numbers of active, encysted and empty tests of *Trinema lineare* (----- encysted tests; ● indicates significant difference from previous ● for active or empty tests; ◆ indicates significant difference from previous ◆ for encysted tests).



5 B

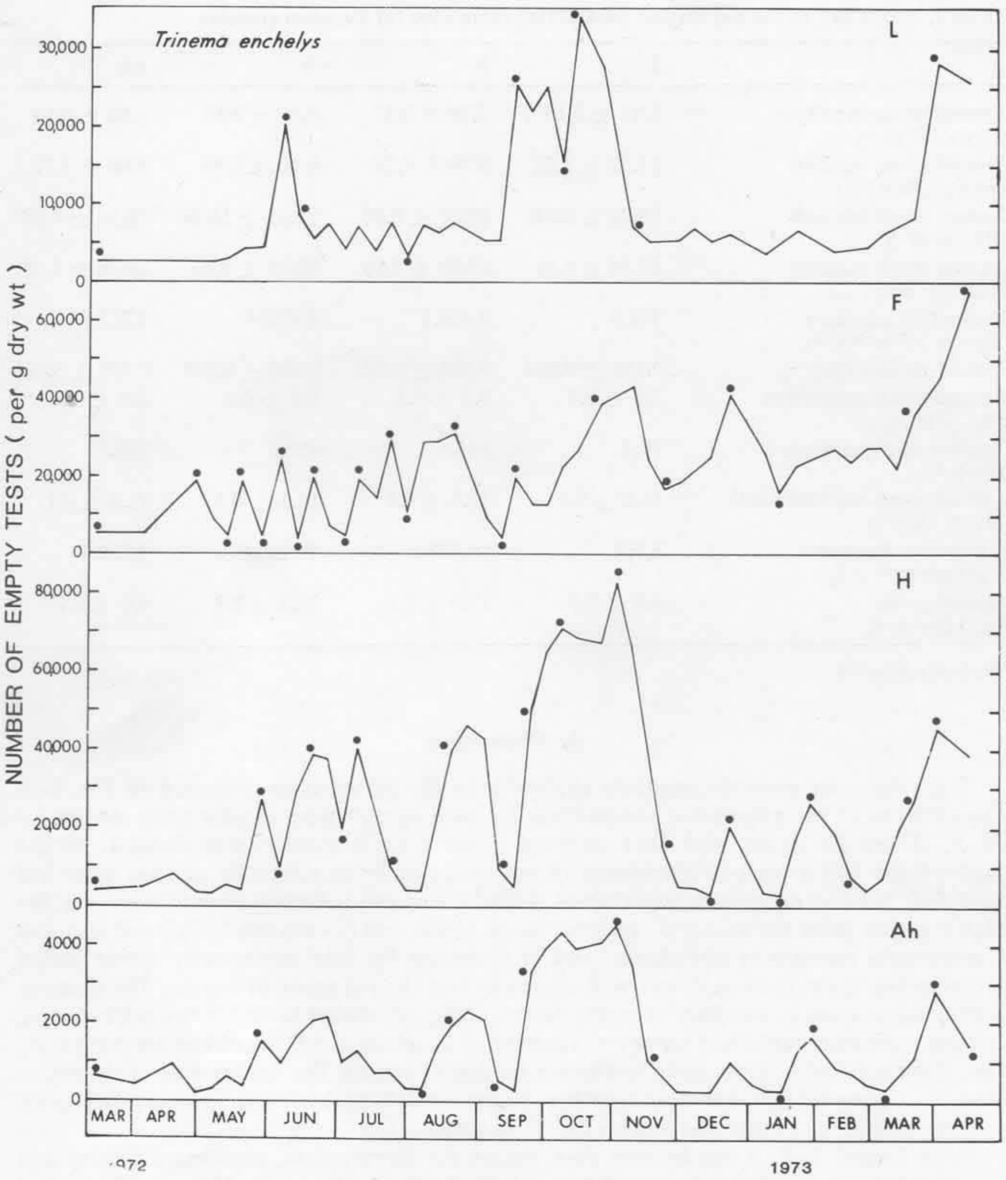
study period, particularly in the spring and summer. Cysts were recorded throughout most of the year in the L, F and H layers and sometimes exceeded active forms in abundance. There was some indication of an inverse relationship between cyst abundance and active abundance.

Despite its abundance being lower than that for *T. lineare*, the annual mean biomass and the annual production biomass for *T. enchelys* far exceeded the totals for all four layers for all the other 14 species. For example, 64% of the total Euglyphidae production biomass and 40% of the total annual $P_B$ were attributable to *T. enchelys*. This species also had the fastest generation times for F- and H-layer species, and the highest mean r (highest mean r recorded in the study), the largest number of generations (largest number in the entire study as well), and the highest $P_B/B$ for all H-layer species. *T. enchelys* was one of only three species not to have its maximum annual weekly mean $P_B/B$ in the F layer. The fastest generation times noted were: L — 1.5 days (early June, mid-September, mid-October), F — 0.9 day (mid-September), H — 1.0 day (late September), and Ah — 1.2 days (late September).



6 A

Fig. 6. The annual fluctuations of numbers of active, encysted and empty tests of *Trinema encelys* (----- encysted tests; ● indicates significant difference from previous ● for active or empty tests; ◆ indicates significant difference from previous ◆ for encysted tests).



6 B

The highest intrinsic rates of natural increase found in the L layer occurred in spring, summer and fall; the other layers, however, showed no seasonal trends. Production biomass peaked in spring and fall in the L and Ah layers but had no seasonal trends in the F and H layers. Production biomass turnover was highest in the spring and fall in the L layer, the spring, summer and fall in the F layer, the summer and fall in the Ah layer, and showed no seasonal trends in the H layer.

Table 7. Summary of the population parameters calculated for *Trinema enchelys*

| | L | F | H | Ah |
|---|---|---|---|---|
| Annual mean density (D) ($\times 10^6$ m$^{-2}$) | 1.91 ± 0.19*) | 4.78 ± 0.47 | 8.30 ± 1.15 | 1.60 ± 0.14 |
| Annual mean relative density (RD) (%) | 14.53 ± 1.52 | 8.30 ± 0.76 | 6.65 ± 0.89 | 8.08 ± 1.17 |
| Annual mean biomass (B) (mg m$^{-2}$) | 18.74 ± 2.21 | 49.31 ± 5.86 | 75.51 ± 10.46 | 35.20 ± 5.38 |
| Annual mean relative biomass (RB) (%) | 40.44 ± 2.51 | 23.23 ± 1.99 | 20.58 ± 2.26 | 24.36 ± 2.26 |
| Production numbers ($P_N$) ($\times 10^6$ m$^{-2}$ y$^{-1}$) | 482.8 | 2,428.1 | 4,603.0 | 1,017.8 |
| Annual mean r (day$^{-1}$) | 0.191 ± 0.014 | 0.304 ± 0.021 | 0.336 ± 0.019 | 0.229 ± 0.018 |
| Annual mean generation time (T) (days) | 5.2 ± 0.7 | 3.3 ± 0.4 | 2.5 ± 0.3 | 5.0 ± 0.8 |
| Number of generations (G) (y$^{-1}$) | 90.4 | 144.6 | 160.2 | 109.3 |
| Annual mean mortality rate (M) (% day$^{-1}$) | 11.2 ± 0.1 | 12.6 ± 0.1 | 13.1 ± 0.1 | 11.8 ± 0.1 |
| Production biomass ($P_B$) (mg m$^{-2}$ y$^{-1}$) | 4,731.1 | 23,795.5 | 45,109.8 | 9,974.4 |
| Annual mean $P_B$/B (week$^{-1}$) | 5.3 ± 0.9 | 13.0 ± 2.7 | 12.3 ± 2.1 | 6.6 ± 1.7 |

*) standard error

## 4. Discussion

There are some general comments applicable to the information presented in Fig. 1—6 The patterns of the population fluctuations for each species were usually quite similar for the F, H and Ah layers, with that observed in the L layer usually quite distinct. All the Euglyphidae had a peak in abundance in autumn, usually immediately or soon after leaf litter fall. All the euglyphids maintained small, active (reproducing) populations over the winter period [also shown for *T. enchelys* in an alpine soil (Laminger 1978)] and also had a substantial increase in abundance (and in r) during the late winter-early spring period before spring thaw (snow-melt was well underway but the soil was still frozen). The patterns of the fluctuations in numbers of empty tests roughly paralleled those for the active forms, perhaps indicating rapid test turnover (Lousier & Parkinson 1981b). When encysted tests were observed, their fluctuations in number tended to parallel the fluctuations of the active tests, i.e., increased and decreased together. Laminger (1978) showed an inverse relationship between numbers of cysts and actives for *T. enchelys*.

From Tables 2—7, it can be seen that, except for *E. cuspidata*, population density and biomass of the Euglyphidae increased with profile depth usually to the H layer. The annual production totals for numbers and biomass, except for *E. laevis*, were highest in the H layer and lowest in the L. *E. laevis* and *T. enchelys* were the only 2 species to have their highest mean intrinsic rate of natural increase and the highest number of generations per year in the H layer; the other species reached these maxima in the F layer. Production biomass turnover was also highest in the F layer for all the species of Euglyphidae.

It can be seen in Table 8 that the 6 constant Euglyphidae species comprised only 33% and 30% of the mean annual abundance and total production numbers respectively, but accounted for 49% of the mean annual biomass and 64% of the total annual production biomass for all species of Testacea. The other 3 species of Euglyphidae were highly intermittent in frequency and comprised less than 2% in total of all 4 statistics just referred to and thus were not included in the calculations. Laminger (1978) found that the Euglyphidae comprised 75% of the total living Testacea in an alpine brown-earths-podsol, about 35% of

Table 8. Comparisons between the 6 constant species of Euglyphidae, the 14 constant species in the total community, and the 28 species comprising the total testacean community

| | | Total for constant Euglyphidae | Totals for the 14 constant species | Totals for all 28 species |
|---|---|---|---|---|
| Mean annual density | L | 6.0 | 17.3 | 17.8 |
| (D) ($\times 10^6$ m$^{-2}$) | F | 24.1 | 62.0 | 64.0 |
| | H | 51.1 | 156.4 | 158.0 |
| | Ah | 4.1 | 20.1 | 20.9 |
| **Total** | | **85.3** | **255.8** | **260.7** |
| Mean annual biomass | L | 28.3 | 36.1 | 46.2 |
| (B) (mg m$^{-2}$) | F | 98.7 | 148.0 | 210.0 |
| | H | 164.2 | 275.8 | 346.1 |
| | Ah | 64.1 | 118.6 | 120.6 |
| **Total** | | **355.3** | **578.5** | **722.9** |
| Production numbers | L | 1,502 | 5,034 | 5,190 |
| ($P_N$) ($\times 10^6$ m$^{-2}$ y$^{-1}$) | F | 7,756 | 19,850 | 20,677 |
| | H | 13,467 | 37,052 | 38,197 |
| | Ah | 4,820 | 25,056 | 26,862 |
| **Total** | | **27,545** | **86,992** | **90,926** |
| Production biomass | L | 6,915 | 8,295 | 14,479 |
| ($P_B$) (mg m$^{-2}$ y$^{-1}$) | F | 37,397 | 48,158 | 59,950 |
| | H | 67,566 | 91,428 | 100,995 |
| | AH | 19,577 | 30,504 | 31,107 |
| **Total** | | **131,455** | **178,385** | **206,531** |

Table 9. Comparison of population parameters for the Euglyphidae from European sites and from the aspen woodland soil

| | Bechwood Soil (1) | Coniferous Soil (1) | Moss under Beech Forest (2) | Beechwood Soil (3) | Ash-Maple Forest (4) | Aspen Woodland Soil (5) |
|---|---|---|---|---|---|---|
| Annual mean density (D) ($\times 10^6$ m$^{-2}$) | 360 | 48.8 | | | 22.3 | 85.3 |
| Annual mean biomass (B) (mg m$^{-2}$) | 324 | 57.8 | | | 352.6 | 355.3 |
| Number of generations (G) (y$^{-1}$) | 43 | 18 | | | | 101 |
| Mortality rate (M) (% day$^{-1}$) | 6.0 | 6.6 | | | | 11.2 |
| Production numbers ($P_N$) ($\times 10^6$ m$^{-2}$) | 5,400 | 1,300 | | | 603 | 27,545 |
| Production biomass ($P_B$) (g m$^{-2}$) | 39 | 6 | 0.09 | 35 | 7.6 | 131 |
| Biomass turnover ($P_B$/B) | 110 | 102 | | | 52 | 369 |

(1) Source: Schönborn (1975): moder humus
(2) Source: Schönborn (1977): moder humus
(3) Source: Schönborn (1978): mull-like moder humus
(4) Source: Schönborn (1982): mull humus
(5) Present Study: mor humus

Table 10. Comparisons between populations of Euglyphidae in European soils and in the aspen woodland soil

| | Shortest T (days) | G ($y^{-1}$) | M (% $day^{-1}$ | B (mg $m^{-1}$ | $P_B$ (mg $m^{-2}$ $y^{-1}$) | $P_B/B$ |
|---|---|---|---|---|---|---|
| *E. rotunda* | | | | | | |
| — beechwood1) | 3.0 | 41 | 5.9 | 31.7 | 3.447 | 108.8 |
| — coniferous1) | 3.0 | 12 | 6.4 | 11.3 | 657 | 59.7 |
| — moss2) | | 21 | 2.6 | | 3.8 | |
| — beechwood3) | | | | | 2.128 | |
| — ash-maple4) | < 2.8 | 12 | 9.7 | 12.4 | 475 | 38.2 |
| — aspen woodland5) | 0.9 | 89 | 10.9 | 19.2 | 7.227 | 376 (9.2)6) |
| *T. lineare* | | | | | | |
| — beechwood1) | 2.2 | 43 | 6.5 | 26.4 | 2,921 | 110.6 |
| — coniferous1) | 2.0 | 24 | 6.8 | 14.6 | 1,385 | 94.9 |
| — moss2) | | | | | 2.5 | |
| — beechwood3) | | | | | 1,876 | |
| — ash-maple4) | < 2.0 | 22 | 11.4 | 17.1 | 690 | 40.3 |
| — aspen woodland5) | 1.2 | 111 | 11.6 | 110.7 | 27,664 | 250 (7.0)6) |
| *T. enchelys* | | | | | | |
| — beechwood1) | 1.6 | 54 | 6.1 | 159.6 | 21,435 | 134.3 |
| — coniferous | 3.5 | 15 | 7.9 | 13.3 | 2,320 | 174.4 |
| — moss2) | | 9 | 2.8 | | 1.4 | |
| — beechwood3) | | | | | 20,700 | |
| — ash-maple4) | < 2.0 | 15 | 15.2 | 139.3 | 2,338 | 16.8 |
| — aspen woodland5) | 0.9 | 126 | 12.2 | 178.9 | 83,611 | 467 (9.3)6) |

1) Source: Schönborn (1975)
2) Source: Schönborn (1977)
3) Source: Schönborn (1978)
4) Source: Schönborn (1982)
5) This study
6) Annual weekly mean for all layers

which belonged to the genus *Trinema*. In an ash-maple mull humus, the Euglyphidae comprised 66, 64, 34 and 29% of the living individuals, production numbers, annual mean biomass and annual production, respectively (Schönborn 1982), and the *Trinema* spp. comprised 77% of the Euglyphidae counted. Several comparisons can be made with the euglyphid study results reported in Schönborn (1975, 1977, 1978, 1982) (Tables 9, 10). Such comparisons showed that the aspen woodland Euglyphidae, despite being less abundant in some instances, generally had higher biomass, much higher production, and a higher number of generations per year (Table 9). Even with *E. rotunda*, the biomass in this study is lower than that from the beechwood soil (Schönborn 1975) but production is more than double in the aspen site (Table 10).

There may be 2 factors which account for the higher euglyphid biomass — a greater relative proportion of *T. enchelys* in this study and possibly higher bulk densities of some or all of the aspen soil layers. The differences in productivity may be attributable to large differences in generation times (Table 10). Despite the low values for mean annual weekly biomass turnover, weekly $P_B/B$ ranged to nearly 400 in some instances (Table 10), particularly at times of prolonged, rapid population growth1).

Using the estimates of secondary production and assuming bacteria as the prime source of food (Stout & Heal 1967; Stout 1973, 1980a, b), it is possible to obtain an approximate estimate of food consumed by testacean populations (Heal 1967; Layborn 1976; Rogerson 1981) (Table 11). The estimate of 876 g $m^{-2}$ $y^{-1}$ of bacteria consumed by the Euglyphidae

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1) see footnote on **p. 330!**

Table 11. Energy budgets for the species of Euglyphidae in the aspen woodland soil

| | | *E. laevis* | *E. rotunda* | *E. scutigera* | *E. cuspidata* | *T. lineare* | *T. enchelys* |
|---|---|---|---|---|---|---|---|
| Mean annual biomass, B ($\times 10^{-3}$) | L | 1.8 | 0.7 | 1.4 | 1.9 | 3.8 | 18.7 |
| | F | 6.8 | 9.1 | 2.2 | 1.1 | 30.2 | 49.3 |
| | H | 8.2 | 8.7 | 10.3 | 1.0 | 60.5 | 75.5 |
| | Ah | 1.4 | 0.7 | 10.6 | — | 16.2 | 35.2 |
| | **Total** | **18.2** | **19.2** | **24.5** | **4.0** | **110.7** | **178.7** |
| Total annual production, $P_B$ | L | 0.2 | 0.1 | 0.2 | 0.3 | 1.5 | 4.7 |
| | F | 2.1 | 3.2 | 0.9 | 0.4 | 6.9 | 23.8 |
| | H | 3.6 | 3.7 | 2.2 | 0.5 | 12.5 | 45.1 |
| | Ah | 0.1 | 0.2 | 2.5 | — | 6.7 | 10.0 |
| | **Total** | **6.0** | **7.2** | **5.8** | **1.2** | **27.6** | **83.6** |
| Total annual respiration losses, R | L | [a] 0.3 (0.1)[b] | 0.2 (0.1) | 0.3 (0.1) | 0.5 (0.2) | 2.5 (0.7) | 7.8 (2.4) |
| | F | 3.5 (1.1) | 5.3 (1.6) | 1.5 (0.5) | 0.7 (0.2) | 11.5 (3.5) | 39.7 (11.9) |
| | H | 6.0 (1.8) | 6.2 (1.8) | 3.7 (1.1) | 0.8 (0.2) | 20.8 (6.3) | 75.2 (22.6) |
| | Ah | 0.2 (0.1) | 0.3 (0.1) | 4.2 (1.2) | — | 11.2 (3.4) | 16.7 (5.0) |
| | **Total** | **10.0 (3.1)** | **12.0 (3.6)** | **9.7 (2.9)** | **2.0 (0.6)** | **46.0 (13.9)** | **139.4 (41.9)** |
| Total annual egestion losses, E | L | 0.8 (0.2) | 0.4 (0.1) | 0.8 (0.2) | 1.2 (0.3) | 6.0 (1.5) | 18.8 (4.7) |
| | F | 8.4 (2.1) | 12.8 (3.2) | 3.6 (0.9) | 1.6 (0.4) | 27.6 (6.9) | 95.2 (23.8) |
| | H | 14.4 (3.6) | 14.8 (3.7) | 8.8 (2.2) | 2.0 (0.5) | 50.0 (12.5) | 180.4 (45.1) |
| | Ah | 0.4 (0.1) | 0.8 (0.2) | 10.0 (2.5) | — | 26.8 (6.7) | 40.0 (10.0) |
| | **Total** | **24.0 (6.0)** | **28.8 (7.2)** | **23.2 (5.8)** | **4.8 (1.2)** | **110.4 (27.6)** | **334.4 (83.6)** |
| Total annual ingestion, I | L | 1.3 (0.5) | 0.7 (0.2) | 1.3 (0.4) | 2.0 (0.7) | 10.0 (3.6) | 31.3 (11.8) |
| | F | 14.0 (5.3) | 21.3 (8.1) | 6.0 (2.3) | 2.7 (1.0) | 46.0 (17.3) | 158.7 (59.5) |
| | H | 24.0 (9.0) | 24.7 (9.2) | 14.7 (5.4) | 3.3 (1.2) | 83.3 (31.3) | 300.7 (112.8) |
| | Ah | 0.7 (0.4) | 1.3 (0.6) | 16.7 (6.2) | — | 44.7 (16.8) | 66.7 (24.9) |
| | **Total** | **40.0 (15.2)** | **48.0 (18.1)** | **38.7 (14.3)** | **8.0 (2.9)** | **184.0 (69.0)** | **557.4 (209.0)** |

[a] Values not in parentheses represent 10 °C, where P = 0.15 I, R = 0.25 I and E = 0.60 I (ROGERSON 1981).

[b] Values in parentheses represent optimum temperatures (15—25 °C), where $P_B$ = 0.4 I, R = 0.2 I, and E = 0.4 I (HEAL 1967; LAYBOURN 1976).

Note: All estimates are wet biomass, mg $m^{-2}$.

amounted to 64% of the total estimated to be consumed by all species of Testacea and represented about 40 times the annual mean standing crop of bacteria. The ratio of secondary production to standing crop of Testacea ($P_B/B$) ranged from 70 to 600, averaging 330 for all euglyphids in all layers. The amount of carbon respired per year by the Euglyphidae was estimated as 22 g $m^{-2}$ (dry mass) ×47% (carbon content of amoebae, Band 1959) = 10.3 g C $m^{-2}$ $y^{-1}$, or 3.8% of the total annual carbon input. This also comprised about 64% of the respiration losses by the total testacean community, indicating that the Euglyphidae are functionally the dominant group of Testacea in the aspen woodland soil.

Schönborn (1965) cultured Testacea on sterile woodland soil and observed humus and litter particles in the food vacuoles of Euglyphidae. Laminger (1978) found that, during periods with near field capacity soil moisture levels, *T. enchelys* ingested primarily bacteria. However, during periods of low soil moisture, *T. enchelys* was observed to ingest mainly detritus particles. While this evidence of detrital feeding cannot be ignored, it is still reasonable to assume (cf., Stout & Heal 1967; Stout 1973, 1980a, b; Bryant *et al.* 1982; Schönborn 1982), that the main source of food for the Euglyphidae, and indeed all of the litter and soil Testacea, would be the bacteria. Given the relatively high moisture content throughout the present study, it appeared that direct impact on the organic cycle by the Euglyphidae was minimal.

## 5. Acknowledgement

Financial support for the study was provided by an NSERC Operating Grant (No. A2257) to Dr. Dennis Parkinson, and an NRCC Postgraduate Scholarship to the author.

## 6. References

Band, R. N., 1959. Nutritional and related biological studies on the free-living soil amoeba, *Hartmannella rhysodes*. J. Gen. Microbiol. **21**, 80—95.

Bonnet, L., & R. Thomas, 1960. Faune terrestre et d'eau douce des Pyrénées Orientales. 5. Thécamoebien du sol. Hermann édit. Paris, 1—104.

Carter, J. H., 1865. On the fresh- and salt-water Rhizopoda of England and India. Ann. Mag. Nat. Hist. **15**, 277—293.

Coûteaux, M.-M., 1976. Dynamisme de l'équilibre des Thécamoebiens dans quelques sols climaciques. Mem. Mus. Nat. Hist. Nat. N. S. sér. A. Zoologie **96**, 1—183.

— 1978. Etude quantitative des Thécamoebiens édaphiques dans une savane à *Loudetia* à Lamto (Côte d'Ivoire). Rev. Ecol. Biol. Sol **15**, 401—412.

— 1979. Le genre *Euglypha:* essai de taxonomie numérique. Protistologica **15**, 565—579.

Decloitre, L., 1962. Le genre *Euglypha* Dujardin. Arch. Protistenk. **106**, 51—100.

— 1976. Le genre *Euglypha*. Compléments à jour au 31 décembre 1974 de la Monographie du genre parue en 1962. Arch. Protistenk. **118**, 18—33.

— 1979. Mises à jour au 31, 12, 1978 des mises à jour au 31, 12, 1974 concernant les genres *Arcella*, *Centropyxis*, *Euglypha* et *Nebela*. Arch. Protistenk. **122**, 387—397.

— 1981. Le genre *Trinema* Dujardin, 1841. Arch Protistenk. **124**, 193—218.

— 1982. Compléments aux publications précédentes mise à jour au 31, XII, 1981 des genres *Arcella*, *Centropyxis*, *Cyclopyxis*, *Euglypha*, *Nebela* et *Trinema*. Arch. Protistenk. **126**, 393—407.

Foissner, W., & H. Adam, 1981. Die Gemeinschaftsstruktur und Produktion der terricolen Testaceen (Protozoa, Rhizopoda) in einigen Böden der Österreichischen Zentralalpen (Hohe Tauern, Glocknergebiet). Veröffentlichungen des Österreichischen MAB — Hochgebirgsprogramms **4**, 53—78.

De Graaf, F., 1956. Studies on Rotatoria and Rhizopoda from the Netherlands. Biol. Jb. Dodonaea **23**, 145—217.

Hall, R. P., & J. B. Loefer, 1930. Studies on *Euglypha*. I. Cytoplasmic inclusions of *Euglypha alveolata*. Arch. Protistenk. **72**, 365—376.

Heal, O. W., 1967. Quantitative studies on soil amoebae. pp. 120—126. In: O. Graff & J. E. Satchell (eds) Progress in Soil Biology. Amsterdam.

— 1970. Methods of study of soil Protozoa. pp. 119—126. In: J. Phillipson (ed.), Methods of study in soil ecology. UNESCO, Paris.

Hedley, R. H., & C. G. Ogden, 1973. Biology and fine structure of *Euglypha rotunda* (Testacea: Protozoa). Bull. Brit. Mus. (Nat. Hist.) Zool. **25**, 119—137.

— & C. G. Ogden, 1974a. Adhesion plaques associated with the production of a daughter cell in *Euglypha* (Testacea: Protozoa). Cell Tiss. Res. **153**, 261—268.

— & C. G. Ogden, 1974b. Observations on *Trinema lineare* Penard (Testacea: Protozoa). Bull. Brit. Mus. (Nat. Hist.) Zool. **26**, 185—199.

— C. G. Ogden, & J. I. Krafft, 1974. Observations on clonal cultures of *Euglypha acanthophora* and *Euglypha strigosa* (Testacea: Protozoa). Bull. Brit. Mus. (Nat. Hist.) Zool. **27**, 103—112.

Laminger, H., 1978. The effect of soil moisture fluctuations on the testacean species *Trinema enchelys* (Ehrenberg) Leidy in a high mountain brown-earths-podsol and its feeding behaviour. Arch. Protistenk. **120**, 446—454.

— K. Geisler-Moroder, A. Siess, E. Spiss, & B. Spiss, 1980. Populationsdynamik terrestrischer Protozoen (Testaceen, Rhizopoda) in zentralalpinen Lagen Tirols. I. Untersuchungen subalpine Böden im Raum Obergurgl (Tirol/Österreich). Arch. Protistenk. **123**, 280—323.

Laybourn, J., 1976. Energy budgets for *Stentor coeruleus* Ehrenberg (Ciliophora). Oecologia (Berl.) **22**, 431—437.

Lousier, J. D., 1974a. Effects of experimental soil moisture fluctuations on turnover rates of Testacea. Soil. Biol. Biochem. **6**, 19—26.

— 1974b. Response of soil Testacea to soil moisture fluctuations. Soil. Biol. Biochem. **6**, 235—239 (Errata — Soil Biol. Biochem. **7**, 185—188).

— 1975. Relationships between distribution of Testacea (Protozoa, Rhizopoda) and the soil habitat. Naturaliste can. **102**, 57—72.

— 1976. Testate amoebae (Rhizopoda, Testacea) in some Canadian Rocky Mountain soils. Arch. Protistenk. **118**, 191—201.

— 1982. Colonization of decomposing deciduous leaf litter by Testacea (Protozoa, Rhizopoda): Species succession, abundance and biomass. Oecologia (Berlin/West) **52**, 381—388.

— 1984. Population dynamics and production studies of *Phyrganella acropodia* and *Difflugiella oviformis* (Testacea, Rhizopoda, Protozoa) in an aspen woodland soil. Pedobiologia **26**, 331—347.

— & D. Parkinson, 1976. Litter decomposition in a cool temperate deciduous forest. Can. J. Bot. **54**, 419—436.

— & D. Parkinson, 1978. Chemical element dynamics in decomposing leaf litter. Can. J. Bot. **56**, 2795—2812.

— & D. Parkinson, 1979. Organic matter and chemical element dynamics in an aspen woodland soil. Can. J. For. Res. **9**, 449—463.

— & D. Parkinson, 1981a. Evaluation of a membrane filter technique to count soil and litter Testacea. Soil Biol. Biochem. **13**, 209—215.

— & D. Parkinson, 1981b. The disappearance of empty tests of litter and soil testate amoebae (Testacea, Rhizopoda, Protozoa). Arch. Protistenk. **124**, 312—336.

— & D. Parkinson, 1984. Annual population dynamics and production ecology of Testacea (Protozoa, Rhizopoda) in an aspen woodland soil. Soil Biol. Biochem. In press.

Netzel, H., 1972. Morphogenese des Gehäuses von *Euglypha rotunda* (Rhizopoda, Testacea). Z. Zellforsch. **135**, 63—69.

— 1977a. Die Struktur des Plättchen-Gehäuses von *Euglypha rotunda* (Rhizopoda, Testacea). Arch. Protistenk. **119**, 191—216.

— 1977b. Die Herstellung des Plättchen-Gehäuses bei *Euglypha rotunda* (Rhizopoda, Testacea). Arch. Protistenk. **119**, 301—324.

Ogden, C. G., 1981. Observations of clonal cultures of Euglyphidae (Rhizopoda, Protozoa). Bull. Br. Mus. Nat. Hist. (Zool.) **41**, 137—151.

Penard, E., 1890. Etudes sur les Rhizopodes d'eau douce. Mém. Soc. Phys. Hist. nat. Genève **31**, 1—230.

Rogerson, A., 1981. The ecological energetics of *Amoebae proteus* (Protozoa). Hydrobiologia **85**, 117—128.

Schönborn, W., 1965. Untersuchungen über die Ernährung bodenbewohnender Testaceen. Pedobiologia **5**, 205—210.

— 1975. Ermittlung der Jahresproduktion von Boden-Protozoen. I. Euglyphidae (Rhizopoda, Testacea). Pedobiologia **15**, 415—424.

— 1977. Production studies on Protozoa. Oecologia (Berlin/West) **27**, 171—184.

— 1978. Untersuchungen zur Produktion der Boden-Testaceen. Pedobiologia **18**, 373—377.

— 1982. Estimation of annual production of Testacea (Protozoa) in mull and moder (II). Pedobiologia **23**, 383—393.

— Beziehungen zwischen Produktion, Mortalität und Abundanz terrestrischer Testaceen-Gemeinschaften. Pedobiologia **25**, 403—412.

Smith, H. G., 1973. The Signy Island terrestrial reference sites: III Population ecology of *Corythion dubium* (Rhizopoda: Testacida) in Site 1. Brit. Antarct. Sur. Bull., Nos. **33/34**, 123—135.

Stout, J. D., 1973. The relationship between protozoan populations and biological activity in soils. Amer. Zool. **13**, 193—201.

— 1980a. Role of Protozoa in nutrient cycling and energy flow. pp. 40—44. In: T. K. Crosby & R. P. Pottinger (eds), 2nd Australasian Conference on Grassland Invertebrate Ecology. Government Printer, Wellington, N.Z.

— 1980b. The role of Protozoa in nutrient cycling and energy flow. Adv. Microbiol. Ecol. **4**, 1—50.

— & O. W. Heal, 1967. Protozoa. pp. 149—195. In: A. Burges & F. Raw (eds), Soil Biology. Academic Press, London.

WAILES, G. H., 1915. Notes on the structure of tests of freshwater Rhizopoda. J. Roy. Micro. Soc. **35**, 105—116.
— & E. PENARD, 1911. Clare Island Survey. Part 65. Rhizopoda. Proc. R. Ir. Acad. **31**, 1—64.

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**Synopsis:** *Original scientific paper*

LOUSIER, J. D., 1984. Population dynamics and production studies of species of Euglyphidae (Testacea, Rhizopoda, Protozoa) in an aspen woodland soil. Pedobiologia **26**, 309—330.

Nine species of Euglyphidae were observed as living cells or empty tests throughout the study period in an aspen woodland soil. Only 6 of these species were identified as constant and they comprised 33 and 30% of the mean annual density and total production numbers respectively for all Testacea, and 49 and 64% of the mean annual biomass and the total annual production biomass for all Testacea. While *Trinema lineare* and *T. enchelys* numerically dominated the Euglyphidae, *T. enchelys* accounted for 64% of the Euglyphidae production biomass and 40% of the total Testacean production biomass. Mean annual biomass and total annual production for the Euglyphidae were estimated as 0.35 and 131 g wet mass $m^{-2}$ respectively, while total annual ingestion, respiration losses and egestion losses were calculated as 876, 219, 526 g wet mass of biomass respectively. The annual production biomass varied from 70 to 600 (mean of 330) times the standing crop of Euglyphidae in all the soil layers. The dry mass of carbon respired annually by the Euglyphidae was estimated as 10.3 g $m^{-2}$, which amounted to 3.8% of the total annual input of carbon.

**Key words:** Protozoa, Testacea, Euglyphidae, biomass, production, ingestion, egestion, respiration, aspen (Populus tremuloides, balsamifera) woodland soil, Canada.

**Footnote to page 326:** (1) SCHÖNBORN (1983) described *T. enchelys* as a highly productive species that can turn over very quickly, i. e., abundance, production aud mortality are high. The present study demonstrates the high productivity potential of *T. enchelys* in natural conditions.